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S. C. J. van der Putte

The Development of the Lymphatic System in Man

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With 33 Figures

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List of Abbreviations

acv	anterior cardinal vein
adr	adrenal gland
als	axillary lymph sac
aut	autonomic nervous tissue
av	azygos vein
baa	branchial arch artery
bp	brachial plexus of nerves
br	bronchus
bt	bifurcation of the trachea
cca	common carotid artery
ce	caudal extension of the jugulo-axillary lymph sac
cia	common iliac artery
cl	clavicula
cv	caudal vein
e	esophagus
eia	external iliac artery
eiv	external iliac vein
ejv	external jugular vein
hav	hemiazygos vein
icv	inferior caval vein
iiv	internal iliac vein
ijv	internal jugular vein
ilp	iliac lymph plexus
isb	intersubcardial anastomosis
itlp	internal thoracic lymph plexus
itv	internal thoracic vein
jals	jugulo-axillary lymph sac
jls	jugular lymph sac
lk	kidney
	lung
ll	lymphatic(s)
llp	lumbar lymph plexus
lv	lumbar vein
mlp	mesenteric lymph plexus
n	nerve
pa	pulmonary artery
pcc	pericardial cavity
pcv	posterior cardinal vein
ptc	peritoneal cavity
ptlp	paratracheal lymph plexus
puv	primitive ulnar vein
ra	renal artery
rv	renal vein
sacv	sacrocardinal vein
sbcv	subcardinal vein
sc	scapula
scla	subclavian artery
sclv	subclavian vein
scmm	sternocleidomastoid muscle
scv	superior caval vein
spcv	supracardinal vein
srv	suprarenal vein
stlp	subtracheal lymph plexus
t	trachea
td	thoracic duct
tm	trapezius muscle
v	vertebra
vv	vein(s), venule(s)
vn	vagus nerve
↓	lymphatico-venous communication

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I. Introduction

When Budge in the eighth decade of the nineteenth century, started his investigations into the origin and development of the lymphatic system, he probably did not expect that these would be the starting-point for disputes that would continue well into our time. But rather than by his results were these disputes intensified by the controversial conclusions of some papers published by Gulland (1894), Ranvier (1897) and Sala (1900), and above all by some new investigations by Sabin (1902–1913) and Huntington (1908–1914) during the first decades of the twentieth century.

The most important controversial point was the difference in opinion about the origin of the lymphatic system. An extensive review of the relevant literature is found in O. F. Kampmeier's book: "Evolution and Comparative Morphology of the Lymphatic System"; Thomas, Springfield, U.S.A. (1969). Whereas some investigators were of the opinion that the lymphatic system was formed from the venous system, there were many others, who believed that this system originates from confluent spaces in the mesenchyme and secondarily communicates with the veins.

The most prominent advocate of the first mentioned opinion was Sabin (1902–1913). She believed that the lymphatics are formed by a process of sprouting from the large central veins in a limited number of definitely localized areas, but that these sprouts demonstrate almost immediately their own lymphatic character. From these sprouts separate primordia develop at first; these enlarge, confluence and form new sprouts which grow out into more peripheral parts of the embryo.

Both Lewis (1905) and Hoyer (1908, 1912, 1934) agreed with her on the venous derivation of the lymphatic system, but their opinions differed from hers in some other respects. Lewis believed that the early lymphatic primordia were formed by long series of isolated, but initially true venous, branches. Hoyer, although accepting Sabin's view concerning their lymphatic character from the beginning, was convinced more or less in accordance with Lewis that these primordia were more numerous than Sabin suggested.

Sabin's theory was strongly attacked by Huntington (1908–1914), McClure (1908–1915) and Kampmeier (1912–1969), who were of the opinion that the lymphatic system does not sprout from already existing veins, but develops independently from them in the mesenchyme. According to these investigators the lymphatics are formed more peripherally in the embryo by confluence of numerous spaces inside the mesenchymal tissue. These lymphatics grow centripetally by annexing other similar spaces. Finally, in certain places, anastomoses

are established with the venous system. The bordering mesenchymal cells become endothelial cells by flattening caused by increasing pressure.

Besides these two oppositional groups there were other, more individual investigators, who occupied a sort of central standpoint (Sala, 1900; van der Jagt, 1932; and Kutsuna, 1933). They believed that the lymphatic system originates both from the veins and from confluent spaces in the mesenchyme. According to them, small venules, isolated from the main venous channels at some specific places, enlarge by coalescence with spaces in the adjacent mesenchyme.

This controverse about the origin of the lymphatic system in general, is reflected in the conclusions drawn from investigations into human development.

Sabin (1909, 1913) discerned two stages in the early development of the human lymphatic system. During the first phase (embryos from 8 to 20 mm C–R length) the "jugular lymph sacs" develop bilaterally just lateral to the confluence of the anterior and posterior cardinal veins. At first, these rather small, sac-like vessels are often distended by blood cells, opening into the veins by small apertures. Within a short period they enlarge greatly, while the communications with the veins continue to exist. During the second phase other lymph sacs, the thoracic duct and the cisterna chyli develop. In the abdomen the retroperitoneal or mesenteric lymph sac was identified ventral to the aorta. It originated, she believed, from the intersubcardinal anastomosis, to extend mainly into the mesentery. Besides this primordium, another paired lymph structure was found, namely the posterior or iliac lymph sac. It is situated lateral to the aorta near the renal veins, from which it seems to have sprouted. Somewhat later, connections are established between these primordia, and by continuance into a cranial direction the cisterna chyli and the caudal part of the thoracic duct are formed. This caudal part meets a downward extension of the left jugular lymph sac, which accompanies the descending aorta from the left to the right side of the embryo. Thus a communication is established between the abdominal and the jugular lymphatics. From this "primary lymphatic system" many sprouts grow outward and invade more peripheral regions.

As mentioned above, Lewis (1909) agreed with Sabin in so far as the venous origin of the lymphatic system was concerned. From observations in the jugular region of human embryos of 10, 11.5, 16 and 22.8 mm C–R length he concluded, however, that the jugular lymph sac of each side is formed by fusion of more, probably up to four, primordia. Sometimes venous communications were observed, but this was not a constant feature. It must be mentioned however, that his assistant Thyng (1914) some years later, while reconstructing an 17.8 mm embryo, could easily detect openings between the large jugular lymph sacs and the veins at the confluence of the internal and external jugular veins. Besides these jugular lymph sacs however, Thyng came upon another lymph sac in this rather young embryo. This also was sac-like in form. It was filled with blood and situated ventral to the abdominal aorta between the superior and inferior mesenteric arteries. It seemed entirely isolated from the nearby intersubcardinal anastomosis. By position is was the mesenteric lymph sac, which apparently developed much earlier than Sabin believed.

In total disagreement with these investigators, Kampmeier (1931, 1960, 1969) was of the opinion that similar to the mode of development of the lymphatic system, as observed by him in some kinds of animals (Kampmeier, 1912, 1915,

1920, 1922, 1925, 1960), the human lymphatic system also was of mesenchymal origin. In human embryos he studied the origin and development of the jugular lymph sacs, the thoracic duct and the cisterna chyli. In the development of the jugular lymph sacs five phases were discerned. During the first phase (embryos from 9 to 12 mm) venous networks grow out from the proximal parts of the anterior cardinal veins into the lateral mesenchyme. These plexuses split up into some vessels, which drain the fore limb, and other sac-like structures often filled with blood, which during the second phase subsequently lose their connections with the anterior cardinal veins until at last only one opening, the most caudal, remains. Then, during the third phase, in the mesenchyme around these isolated veins, named by him "venolymphatics", numerous vacuoles appear, which enlarge and fuse with one another. During the next phase this process continues, true lymphatics being formed, which are entirely seperated from the venous system and contain in their lumina the remnants of the wall of the "venolymphatics". It is not until the embryos have reached a length of 30 mm that new and definitive lymphatico-venous communications are established at the jugulo-subclavian confluence. After that, the lymph sacs become filled up for the most part by the development of lymphoid tissue in walls and septa. The rest of the sacs form the jugular lymph truncs and the upper part of the thoracic duct (right lymphatic duct).

In embryos from 20 to 30 mm the thoracic ducts and the cisterna chyli develop in essentially the same way. The thoracic ducts develop bilaterally by confluence of vacuoles in the mesenchyme just outside degenerating and shringing veins dorsomedial to the anterior cardinal veins and ventral to the azygos and hemiazygos veins. More caudally, the cisterna chyli is formed in quite the same way around regressing parts of the supracardinal veins at the level of the kidneys. Kampmeier did not describe the origin of other parts of the abdominal lymphatic system.

According to Balankura (1951), their mode of origin is completely the same as described by Kampmeier as regards the cisterna chyli. Balankura rejected the idea of separate lymph sacs as given by Sabin.

From investigations into the origin and development of the vasa sanguinea vasorum of the wall of the descending aorta (van der Putte, 1969) some questions remained particularly about the origin and development of the lymph vessels of this region. At first, no problems were met, probably because embryos larger than 30 mm C-R length were involved. However by subsequently studying younger embryos, the observations were no longer in accordance with those reported in the relevant literature, i.c. Kampmeier's observations. Meanwhile, it became evident that our knowledge about the development of the human lymphatic system was far from complete and re-study of this particular problem seemed to be fully justified.

II. Material and Methods

In this investigation 40 human embryos between 8 mm total length and 33 mm C-R length (estimated ages between 35 and 65 days after fertilization) were examined. Part of the material was kindly lend by other institutes, another part was prepared by the author

Table 1. Data concerning the embryos studied

Number	Age of embryos in days	Length of embryos in mm*	Fixation	Direction of section	Thickness in microns	Remarks
T 52799	—	8	Formalin	Transverse	5	Tubal pregnancy
T 97551	—	8	Formalin	Transverse	14	Tubal pregnancy
E 1	—	10	Formalin	Transverse	10	Spontaneous abortion
BPA 108	42	11	Bouin-d'Hollande	Transverse	7	Curettage
S 39	—	11	Formalin	Transverse	10	Tubal pregnancy
ME	—	12	Formalin	Coronal	10	
S 4	—	12	Formalin	Transverse	10	
T 32530	—	13	Formalin	Sagittal	14	Ectopic pregnancy
S 10	—	13	Formalin	Transverse	10	Spontaneous abortion
BPA 113	44	13	Formalin (Holt)	Transverse	7	Curettage
E 153	—	14	Formalin	Transverse	10	Spontaneous abortion
S 62	—	14	Formalin	Transverse	14	Spontaneous abortion
T 81793	—	14	Formalin	Transverse	14	Ectopic pregnancy
BPA 112	46	14	Formalin (Holt)	Transverse	7	Curettage
S 8	—	15	Formalin	Transv./sag.	10	Spontaneous abortion
T 127776	—	15	Formalin	Sagittal	14	Ectopic pregnancy
E 65	—	16	Formalin	Transverse	10	Curettage
E 162	—	17	Formalin	Transverse	10	Ectopic pregnancy
BPA 101	47	17	Bouin-d'Hollande	Transverse	7	Curettage
S 9	—	17	Formalin	Transv./sag.	10	Spontaneous abortion
T 132870	—	18	Formalin	Sagittal	14	Ectopic pregnancy
BPA 107	51	19	Bouin-d'Hollande	Transverse	7	Curettage
T 86663	—	20	Formalin	Transverse	14	Curettage
S 47	—	20	Formalin	Transverse	10	Spontaneous abortion
S 51	—	21	Formalin	Transverse	10	Spontaneous abortion
E 13	—	22	Bouin	Transverse	10	Ectopic pregnancy
S 83	—	22	Formalin	Transverse	10	Spontaneous abortion
BPA 104	56	22	Formalin	Transverse	7	Curettage
BPA 109	56	22	Bouin-d'Hollande	Transverse	7	Curettage
BPA 100	54	22	Bouin-d'Hollande	Transverse	7	Curettage
S 50	—	23	Formalin	Transverse	10	Spontaneous abortion
BPA 111a	56	23	Bouin-d'Hollande	Transverse	7	Curettage; one of gemelli
BPA 111b	56	23	Bouin-d'Hollande	Transverse	7	Curettage; other of gemelli
E 139	—	24	Formalin	Transverse	10	Spontaneous abortion
BPA 102	60	—	Bouin-d'Hollande	Sagittal	7	Curettage
E 41	—	25	Carnoy	Transverse	10–20	
PL 4198	—	26	Formalin	Transverse	10	Spontaneous abortion
BPA 106	63	—	Bouin-d'Hollande	Transverse	7	Curettage
BPA 30	—	31	Formalin	Transverse	10	Spontaneous abortion
1472	—	33	Formalin	Transverse	7	Spontaneous abortion

* Embryos more than 15 mm in length were measured by their C–R length.

himself (Table 1)[1]. These embryos were fixed in Bouin's fixative (modified after D'Hollande) or in a 10 per cent formaldehyde solution neutralized by $CaCl_2$, buffered by phosphate and corrected as to its osmolarity by sucrose. The material was properly progressed, embedded in paraplast and serially sectioned at 7 microns. All embryos, except one, were cut transversely, because the axial structures were the most helpful landmarks for finding and following the often inconspicuous and variable lymphatics. Because no specific staining for the early lymphatic endothelium was available, a routine general tissue staining, namely Ehrlich's haematoxylin and azophloxin 0.05 per cent was employed.

In order to obtain reliable results from this rather simple method, it was of the utmost importance that series of sections were available of which the completeness was beyond any doubt. For, whereas in the elder embryos the lymphatics in most cases were easy to identify because of their appearance as large-meshed networks of irregular and wide thin-walled vessels, which suddenly may narrow considerably and never contain many blood cells, great problems were met in respect of the lymphatics in younger embryos. In these embryos some of the above mentioned characteristics are often missing in varying grades, and even if they do show up, they may be much less marked than in the elder ones. Besides, they may even differ in one and the same embryo and in different embryos of the same age. Fortunately all lymphatics have, besides these irreliable features, one characteristic in common, which can always be found, namely their almost complete isolation from the blood vessels. This is due to the fact that, although both structures are often lying very close together, not more than one or two very small and split-like connections between the two could be found. Before inferring to the occurrence of two seperate or almost separate vascular structures certainty about the completeness of the series had to be established beyond doubt. It was for this reason that the own material was prepared by the author himself.

For demonstrational purpose the main blood and lymph vessels of ten selected embryos were reconstructed by a method that is essentially the same as Gruenwald (1938) used in his study of the development of the inferior caval vein.

III. Observations

In the embryos collected and prepared as described, it was possible to study the development of the lymphatic system from the very beginning, when only a few inconspicuous small vessels could be found, up to the phase when all main lymph truncs known from the adult were completed.

Although in the development of the lymphatic system real distinct phases are lacking, it seemed desirable to make a division into 5 phases in order to obtain an appropriate description.

A. First Phase (Embryos from 8 to 12 mm Total Length)

Whereas in the youngest embryos of 8 mm on lymph vessels could be identified, in somewhat older embryos vascular structures were found, whose lymphatic character at one time was rather questionable and at another time was unmistakebly true.

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1 The T-numbered embryos belong to the collections of the Laboratory of Pathology, Department of Neuropathology (Head: V. D. W. Schenk, M.D.) and the Department of Anatomy (Head: Prof. J. Moll, M.D.) of the Erasumus University of Rotterdam; the E-numbered embryos are part of the collection of the Department of Anatomy and Embryology of the University of Utrecht (Head: Prof. W. J. van Doorenmaalen, M.D.); and the S-numbered embryos were lend from the collection of the Department of Anatomy and Embryology of the University of Leiden (Heads: Prof. J. Dankmeier M.D. (†) and Prof. J. M. F. Landsmeer).

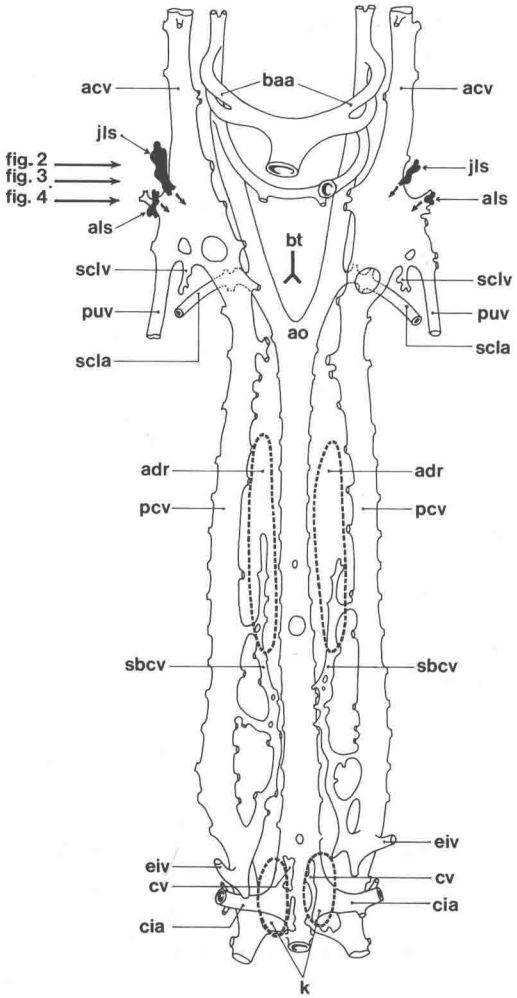

Fig. 1. × 35. Graphic reconstruction of the large prevertebral blood vessels and first lymphatic primordia of an 11 mm embryo, anterior view. The early jugular (*jls*) and axillary (*als*) lymph sacs are rather inconspicuous and blind-ending vessels communicating with the anterior cardinal veins (*acv*) via small and split-like apertures (↓)

The first lymphatics were observed in the rather extensive jugular region, where a short while before the large blood vessels had developed (Fig. 1). Here, the arterial system consists of the bilaterally symmetric branchial arteries bending dorsally to the dorsal aortae. From these aortae the dorsal intersegmental arteries arise, of which those originating just cranial to where both aortae fuse, are about to form the small subclavian arteries. Just lateral to the aortae the wide anterior cardinal veins are situated. These continue cranially into the head veins, receiving all blood from the rest of the head and from the neck region by several, mainly small, venules. These venules may be divided into the segmentally arranged dorsal branches, medial branches from the oesophageal, tracheal and bronchial structures and the vagus nerves, a few ventral branches

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